FURTHER OBSERVATIONS ON PENTASTOMIDS (ARTHROPODA) PARASITIC IN AUSTRALIAN REPTILES AND MAMMALS

J. RILEY & D. M. SPRATT

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A collection of adult and nymphal pentastomids representative of at least four genera is described. Two species of *Raillietiella* and one species of *Parasambonia* from snakes (*Pseudechis australis, Pseudonaja textilis* and *Cryptophis nigrescens*) are probably new, but more specimens are required before their status can be confirmed. Mature and immature *Waddycephalus longicauda, W. superbus* and *W. punctulatus* (all Riley & Self 1981) are identified from snake hosts but specific determination of five lots of specimens was not possible. Evidence endorses an earlier suggestion that there may be two species of *Waddycephalus* in tiger snakes; *W. scutata* from island populations and an unnamed species from mainland populations of the *Notechis scutatus/ater* complex. Nymphal specimens of *Waddycephalus* from marsupials (*Parantechinus apicalis* and *Dasykaluta rosamondae*), a snake (*Cryptophis nigrescens*), a gecko (*Heteronotia binoei*), a skink (*Hemiergis decresiensis*) and frogs (*Ranidella remota* and *Palmatorappia solomonis*) all bear characteristic double hooks. The accessory spine above the hook arises from a point midway between the hook and the fulcrum and appears to be an integral and functional part of the hook. *Armillifer australis* Riley & Self, 1981 is described from infections in four pythons (*Morelia amethistina* and *Morelia spilota*); the latter is a new host record. A single nymph recorded from the body cavity of *Rattus leucopus* is identified as *A. australis* on the basis of abdominal annulus counts.

J. Riley, Department of Biological Sciences, University of Dundee, Dundee DD1 4HN, Scotland, U.K. & D. M. Spratt, Division of Wildlife and Rangelands Research, CSIRO, P.O. Box 84, Lyneham, A.C.T. 2602. Manuscript received 21 October 1986.

In an historical review of Australian Pentastomida, Riley, Spratt & Presidente (1985) recorded seven genera comprising 17 species occurring in Australian reptiles and mammals, and identified nymphal *Waddycephalus* spp. and *Armillifer* spp. from marsupials. This paper reports primarily on a pentastomid collection in the South Australian Museum (SAM) and describes further adult and nymphal material, attributed to the genera *Waddycephalus* and *Armillifer*, from reptiles, amphibians and mammals. The double nature of the hook of nymphal *Waddycephalus* (Riley *et al.* 1985) is confirmed, as are earlier observations (Riley & Self 1981b) of significant anatomical differences between mainland and island forms of *Waddycephalus* infecting the same species of snake. Two large raillietiellids and two parasambonids from snakes are described, however more material is required before their specific status can be confirmed as new.

MATERIALS AND METHODS

The material examined in this study was collected primarily in eastern mainland Australia, Tasmania and neighbouring offshore islands. It is supplemented by nymphal *Waddycephalus* (or *Elenia*?) spp. from the Solomon Islands and New Guinea.

The methods are those outlined in Riley *et al.* (1985) and the hooks of raillietiellids were measured according to the convention of Ali *et al.* (1982) i.e. barb length AB (notation AD in error, p. 42, Riley *et al.* 1985), shank length BC. Overall hook length of the double hooks of nymphal *Waddycephalus* spp. was measured according to the convention illustrated in Figure 2. All measurements are in micrometers with the exception of body length, which is in millimetres. Most specimens are deposited in the South Australia Museum (SAM), Adelaide; two lots are deposited in the Queensland Museum (QM), Brisbane. Reptile nomenclature follows Cogger, Cameron & Cogger 1983; dasyurid marsupial nomenclature follows Archer 1982.

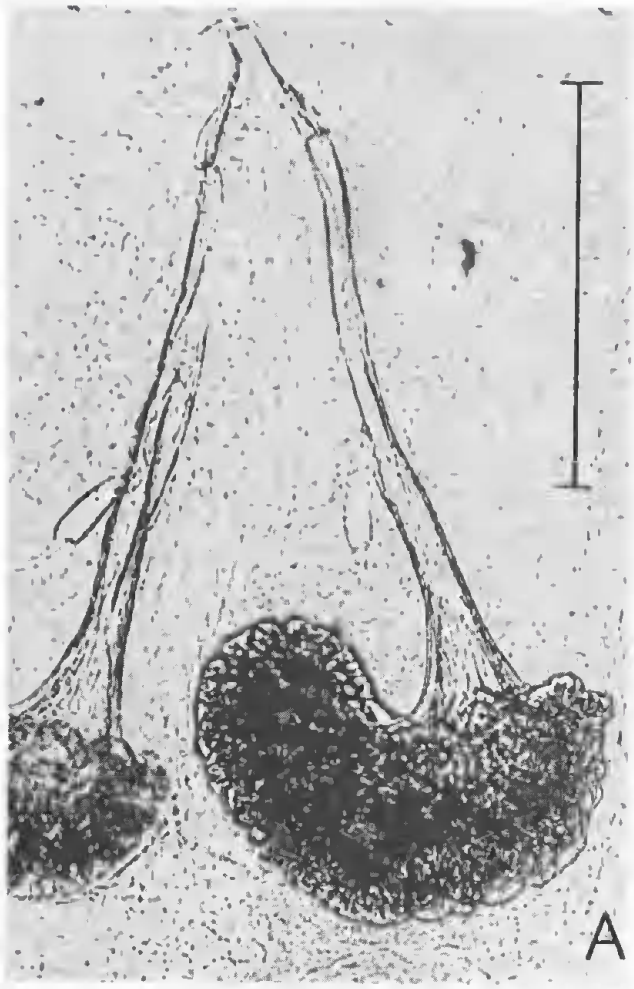
Order CEPHALOBAENIDA

Raillietiella spp. from snakes

Raillietiella sp. a

Material Examined

From lung of *Pseudechis australis* (Gray), locality unknown (died in Melbourne Zoo), in SAM No. N1980183.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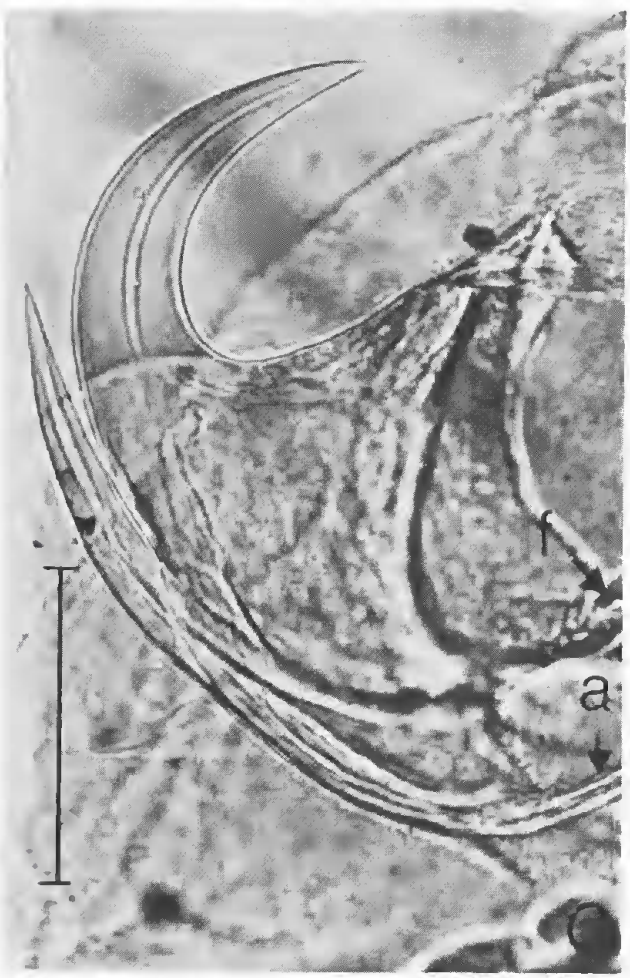
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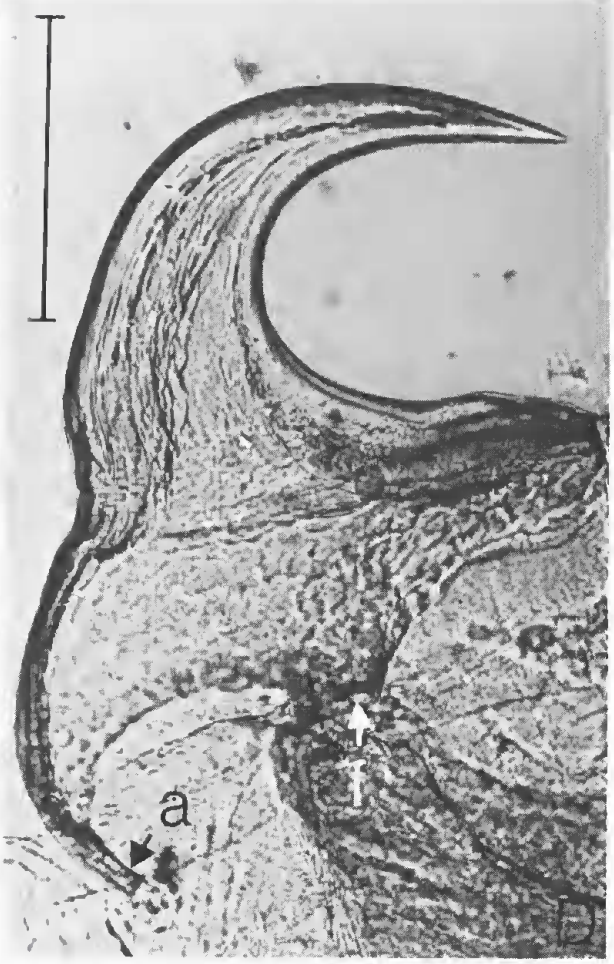
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Description

Female (n = 4). Length 33–52 ($\bar{x}$ = 42), with 45 or 6, 41 or 2, 36 (?) and 39 (?) annuli respectively. Posterior hook of 52 mm specimen, AB 240, BC 370.

Male (n = 1). Length approx. 9, annuli uncountable and therefore slide-mounted. Posterior hook, AB 135; BC 220. Base of copulatory spicule massive, maximum diameter 520 and covered with a reticulum of tubular elevations (Fig. 1A).

Discussion

The heavily ornamented male spicule, 520 μm across at the base (Fig. 1A), is virtually identical to those of *R. orientalis* and *R. agcoi* (Ali, Riley & Self 1982). *R. orientalis* infects colubrid, viperid and elapid snakes in south-east Asia and Taiwan whereas *R. agcoi* is found only in cobras in the Philippines. The females of these two species are distinguished in a number of ways: the former has bigger hooks (see Fig. 3, in Ali *et al.* 1982), more annuli (33–47 *contra* 30–35) and is generally longer and stouter than *R. agcoi.* The overall shape of the present species, and its hooks, are reminiscent of *R. agcoi* but its annulus count, though variable, is within the range of *R. orientalis.* The host, the king brown snake, *Pseudechis australis*, is an endemic species and its raillietiellid parasite may be unique by virtue of geographic isolation. This is probably a new species, but, because it combines important characteristics of these two closely related species we have left it unnamed, pending more specimens and more refined diagnostic techniques.

Raillietiella sp. ***b***

Material Examined

From lung of *Pseudonaja textilis* (Duméril, Bibron & Duméril), Townsville, Queensland, in SAM No. N1985149.

Description

Female (n = 2). One headless abdomen; length other specimen 50, annuli uncountable, specimen therefore slide-mounted. At least 30–40% of eggs in uterus contain fully-developed primary larvae; the specimen is therefore mature. One posterior hook measured, AB 400; BC 510.

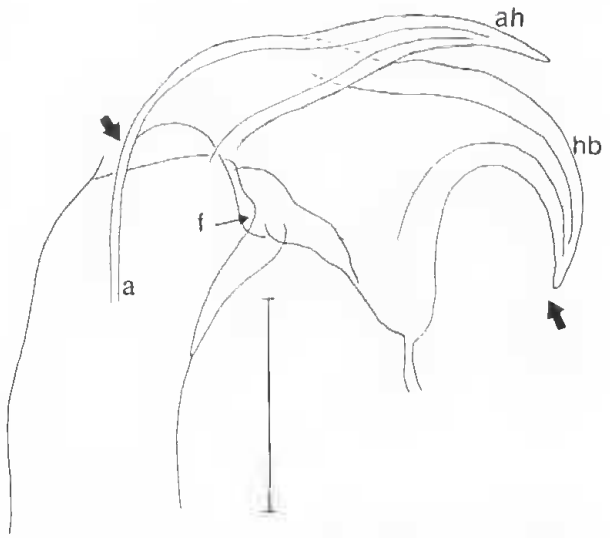

FIGURE 2. Diagrammatic representation of hook of nymphal *Waddycephalus* sp. The distance between the larger arrows indicates our measurement of the overall length (a = apodeme; ah = accessory hook; f = fulcrum; hb = hook barb) (scale bar = 120 μm).

Discussion

Apart from the species recorded above, only two raillietiellids are known from Australia; *R. amphiboluri* from the bearded dragon, *Amphibolurus barbatus* (Cuvier), (Mahon 1954, Riley *et al.* 1985) and *R. scincoides* from the eastern blue-tongued lizard, *Tiliqua scincoides* (White), (Ali, Riley & Self 1984): the latter has blunt-tipped posterior hooks and *R. amphiboluri* is smaller than the present species with much smaller hooks (AB 200–220; BC 370) (Ali *et al.* 1985) (notation AD in error).

The intact specimen clearly belongs to the Group VI taxon of raillietiellids (Ali *et al.* 1985) which includes all of the species from snakes. The two species, *R. orientalis* from south-east Asia and Indonesia and *R. agcoi* from the Philippines are, zoogeographically, most proximate to the present specimen, but it has much longer hook barbs (dimension AB) than either of these species (compare with Fig. 3 in Ali, Riley & Self 1982). This is almost certainly a new species but the poor state

FIGURE 1. A. Copulatory spicules of male *Raillietiella* sp. from *Pseudechis australis* showing massive base covered with tubular elevations (scale bar = 500 μm). B. Cephalothorax of male nymph of *Waddycephalus* sp. from mesentry of *Satanellus hallucatus* [described by Riley *et al.* (1985)]. The double nature of the outer hooks is obvious but the inner hooks are not in the plane of focus (m = mouth) (scale bar = 500 μm). C. Outer hook of nymph of *Waddycephalus* sp. from *Hemiergis decresiensis* showing spinous extension. The back of the extension forms a long apodeme (a) (f = fulcrum) (scale bar = 100 μm). D. Hook of adult *Armillifer* sp. from python (S.A.) illustrating typical unornamented porocephalid hook (a = apodeme; f = fulcrum) (scale bar = 200 μm).

of preservation and lack of males precludes specific identification.

Order **POROCEPHALIDA**

Parasambonia spp. from snakes

Parasambonia bridgesi Riley & Self

Material Examined

From lung of *Pseudechis porphyriacus* (Shaw), Healesville Sanctuary, Victoria, in SAM No. N1980173.

Description

Female (n = 2). Length 26, with 50 and 54 pre-vaginal and post-vaginal annuli.

Male (n = 1). Length 7, with 53 annuli.

Discussion

There are no uncertainties regarding the status of these specimens. All of the characters fall well within the ranges described for *P. bridgesi* by Riley & Self (1982).

Parasambonia sp. ***a***

Material Examined

From lung of *Austrelaps superbus* (Günther), 5 km south of Bowral, New South Wales, in SAM No. N1986192.

Description

Male (n = 1 plus 2 anterior ends). Length 8, with 51 annuli. Heads slide-mounted, outer hook with finger-like extension, AD 175, 190; BC 95, 100.

Discussion

The outer hooks possess the projecting spine characteristic of the genus *Parasambonia*. The low annulus count is more characteristic of *P. minor* than *P. bridgesi*, however the hook dimensions are much smaller than those of *P. minor*, the dimensions of which do not overlap with the much larger hooks of *P. bridgesi* (Riley & Self 1982). The absence of fully gravid females precludes confident specific identification. *P. minor*, but not *P. bridgesi*, has been recorded from the copperhead (Riley & Self 1982).

Parasambonia sp. ***b***

Material Examined

From lung of *Cryptophis nigrescens* (Günther), Mogo S.F., New South Wales, in SAM No. N1986191.

Description

Female (n = 1). Length 29, annuli uncountable. Outer hook with projecting spine, AD 465; BC 245.

Discussion

Hook dimensions in this gravid specimen are larger than those reported in species of *Parasambonia* from Australian snakes (Riley & Self 1982), suggesting that it represents a new species. Additional specimens in good condition are required to resolve this matter. The stomach of this small-eyed snake contained a partly-digested eastern water skink, *Sphenomorphus quoyii* (Duméril & Bibron).

Waddycephalus spp. from snakes

Waddycephalus longicauda Riley & Self

Material Examined

From lung of *Demansia psammophis* (Schlegel), Queensland National Parks and Wildlife Service, Moggill, Queensland, in QM No. W12193.

Description

Female (n = 1). Length 27, with 49 pre-vaginal and 7 post-vaginal annuli, preadult.

Male (n = 6). Length 8–11, with 56–59 annuli ($\bar{x}$ = 57).

Discussion

The features of this material, particularly the long and finely tapered post-vaginal tail, are characteristic of *W. longicauda* (Riley & Self 1981b).

Waddycephalus sp. ***a***

Material Examined

From lung of *Pseudonaja textilis* (Duméril, Bibron & Duméril) taken at Halls Gap, Grampians, Victoria, in SAM No. N1980204.

Description

Female (n = 1). Length 37, with 63 pre-vaginal and 4 post-vaginal annuli. Hooks removed from one side, BC 530, 540; AD 860, 890.

Discussion

The only pentastomid described from *P. textilis* is a female which was tentatively identified as *W. porphyriacus* purely on the basis of similarities in annulus counts: hooks were not measured (Riley & Self 1981b). The present fully mature specimen has far fewer pre-vaginal annuli (63 *contra* 75) than the type series of *W. porphyriacus*. Hook dimensions are very much smaller than those of *W. porphyriacus* and similar to *W. superbus* from a

copperhead, *Austrelaps superbus* (Günther), and to an unnamed species from a mainland tiger snake, *Notechis scutatus* (Peters) (Riley & Self 1981b). Two other characters, the number of annuli and the attenuated caudal extremity, also place it close to these species. However, the type series of *W. superbus* was derived from copperheads taken in Tasmania and nearby islands (Riley & Self 1981b), as was a more recently described infection (Riley *et al.* 1985). To date, *W. superbus* is recognised only as an island species, although copperheads are known on the mainland where their range overlaps that of *P. textilis*. Different dietary preferences have been reported in these snakes (Cogger 1983) however, the food habits of different populations of a snake species over its geographic range are not well known. Recent evidence suggests strongly that dietary preference is different in regions where food resources are skewed or limiting (Schwaner 1985). Until more specimens become available the status of the *Waddycephalus* from *Pseudonaja textilis* remains uncertain.

Waddycephalus sp. *b*

Material Examined

From lung of *Notechis ater niger* Kinghorn, Reevesby I., South Australia, in SAM No. N1985151.

Description

Female (n = 2). Both specimens in very poor condition, length about 36–38, no detail of annulation could be discerned. Hooks from one specimen, BC 400, 410; AD 705, 690.

Discussion

The hooks are much smaller than those of all recognised species of *Waddycephalus* except *W. scutata*, also taken from a tiger snake, on St Francis Island, South Australia. Riley & Self (1981b) recorded the host of the type as *Notechis scutata* (= *scutatus*), based on the collector's label in the vial. Cogger (1983) recognised *N. scutatus* as a purely mainland species being replaced by *N. ater* on islands off the coast of South Australia. However, recent studies of morphological variation in tiger snakes on Kangaroo Island have revealed banded, unbanded, red-bellied and melanistic forms believed to belong to the same species complex (Schwaner 1984). Thus *W. scutata* is currently recognised as a parasite only of island populations of the *N. scutatus/ater* complex, its principal distinguishing characteristic being its particularly small hooks. Hook dimensions in the present specimens form a cluster distinct from *W. scutata* (compare with Fig. 6 in Riley & Self 1981b and below) and suggestive of a new species of *Waddycephalus*.

Waddycephalus sp. *c*

Material Examined

From lung of *Notechis scutatus* (Peters), Grampians, Victoria, in SAM No. N1980171.

Description

Female (n = 7). Length 32–43 ($\bar{x}$ = 38), with 60–63 pre-vaginal ($\bar{x}$ = 61.5) and 2–5 ($\bar{x}$ = 3.2) post-vaginal annuli. Hooks taken from one side of 32 mm and 40 mm females, BC 495, 535; AD 885, 910 respectively.

Male (n = 4). Length 14–20 ($\bar{x}$ = 16), 62–68 annuli ($\bar{x}$ = 64).

Discussion

In their review of the genus *Waddycephalus* Riley & Self (1981b) separated the species from tiger snakes (*Notechis* spp.) into two groups distinguished principally by marked differences in hook size: small hooks are characteristic of *W. scutata* from island populations of the *Notechis scutatus/ater* complex whereas larger hooks are found in specimens from mainland tiger snakes (see Fig. 6 in Riley & Self 1981b). They concluded that geographical isolation was responsible for the observed differences and that two hosts may be involved. The present findings substantiate these differences and combine to suggest indeed that there may be two species of *Waddycephalus* infecting tiger snakes. More sophisticated diagnostic techniques, preferably utilizing live material, are required to confirm this postulate.

Waddycephalus superbus Riley & Self

Material Examined

From lung of *Austrelaps superbus* (Günther), (a) Launceston, (b) Longford, Tasmania, in SAM Nos. (a) N1980175, (b) N1980205.

Description

Female (a) (n = 3). Length 37–41, with 59–63 pre-vaginal and 3–4 post-vaginal annuli. Hooks from one side of 40 mm specimen, BC 530, 580; AD 900, 970.

Female (b) (n = 2). Most of abdomens missing, annuli uncountable; both apparently mature. Hooks dissected from one side of both females, BC 525, 525; AD 840, 840 respectively.

Male (b) (n = 1). Length 15, possibly 62 annuli.

Discussion

These specimens are very similar to the type series of *W. superbus* (from the same host species also taken in Tasmania) except that one specimen from Launceston has two more abdominal annuli and the hooks are slightly larger than those described by

Riley & Self (1981b) and Riley *et al.* (1985). Nevertheless, all of the hook dimensions measured to date combine to form a discrete cluster group and this species at least, is now well characterized. All specimens recovered thus far come from Tasmania, endorsing the suggestion that *Waddycephalus teretiusculus* Baird, 1862, the type species of the taxon and also occurring in the copperhead, is probably a mainland species (Riley & Self 1981b, Riley *et al.* 1985). Lungs of specimens of *A. superbus* held in the Australian National Wildlife Collection were examined for *W. teretiusculus* from the following mainland localities (numbers of specimens in parentheses) but pentastomids were not recovered: Mt Gingera, ACT (1); Ginini Flats, ACT (1); Captain's Flat, NSW (3); Pepper Creek on Big Badja Mountain via Numeralla, NSW (1); Kosciusko National Park near Kiandra entrance (1) and near Peak River, NSW (1); Tumbarumba, NSW (1); Portland, Vic. (2); Flinders I. (1).

Waddycephalus sp. *d*

Material Examined

From lung of *Drysdalia coronoides* (Günther), Fenelon I., South Australia, in SAM No. N1985152.

Description

Female (n = 1). Immature, slide-mounted. Length 10, with 56 pre-vaginal and 5 post-vaginal annuli. Hook measurements BC 280, 300; AD 430, 420.

Male (n = 1). Immature, slide-mounted. Length 9, with 64 annuli.

Discussion

The host snake was originally recorded as *Denisonia coronoides* but species of *Drysdalia* were formerly included in the genus *Denisonia*. The immature state of the present specimens precludes specific identification.

Waddycephalus punctulatus Riley & Self

Material Examined

From lung of *Dendrelaphis punctulata* (Gray), Northern Territory, in SAM No. N1985153.

Description

Female (n = 1). Length 33, with 52 pre-vaginal and 11 post-vaginal annuli.

Male (n = 1). Length 14, possibly 61 annuli.

Discussion

There is no confusion concerning the status of these specimens from the common tree snake; their size and annulus number agree well with the original description of *W. punctulatus* (Riley & Self 1981b).

Waddycephalus sp. *e*

Material Examined

From lung of *Morelia spilota* (Lacépède), St Francis I., South Australia, in SAM No. N1985154.

Description

Female (n = 1). Immature, length 9.5, with 52 pre-vaginal and 4 or 5 post-vaginal annuli.

Discussion

The anterior part of the cephalothorax, including the pair of inner hooks and the mouth are missing. The outer hooks lack the projecting spine characteristic of *Parasambonia* spp. (Riley & Self 1982). The position of the vagina places the specimen in the family Sambonidae and the annulus count indicates that it is a species of *Waddycephalus* but, it has far fewer annuli than the immature female described previously from the same host species and tentatively identified as *W. porphyriacus* (Riley & Self 1981b).

Nymphal **Waddycephalus** spp.

Material Examined

(i) from *Parantechinus apicalis* (Gray), locality unknown, in SAM No. N1980210.

(ii) Encysted in a skink, *Hemiergis decresiensis* (Cuvier), South Australia, in SAM No. 1985155.

(iii) Encysted in abdomen of *Dasykaluta rosamondae* Ride (a) Woodstock Station, (b) Abydos Station, near Marble Bar, Western Australia, in SAM Nos. (a) N1985156, (b) N1980182.

(iv) One nymph, from below post-orbital skin of a frog, *Ranidella remota* Tyler & Parker, Papua New Guinea, in SAM No. N1985157.

(v) 14 nymphs encysted in intestinal connective tissue of *Cryptophis nigrescens* (Günther), Mogo S.F., New South Wales, in SAM No. N1986190.

(vi) 3 nymphs encysted in gecko, *Heteronotia binoei* (Gray), Girraween National Park, Wyberba, Queensland, in QM No. W12194.

Description

(i) Three nymphs dissected from cysts and slide-mounted. Length about 6, 1 specimen (sex unknown) with 74 annuli, 1 male with 70 annuli. All hooks double, overlain by accessory spine (Fig. 2) the base of which arises from a point between fulcrum and hook. Spine an integral part of hook and attached to fulcrum only by thin, flexible sheet of cuticle. Overall hook length (measurement as illustrated in Fig. 2) 300–340.

(ii) Three nymphs dissected from cysts and slide mounted. Length about 4–5, with 62–63 annuli, sex indeterminable. Hooks double, overall length 210–250 (Fig. 1C).

(iiia) All dissected from cysts and slide-mounted. Length about 6, with 56–62 annuli ($\bar{x}$ = 60). Hooks double, overall length 250–280.

(iiib) Six small cysts opened and nymphs slide-mounted, large composite cyst containing many larvae left intact. Length 4–5, with 56–59 annuli (3 counted). Hooks double, overall length 230–260.

(iv) Male nymph, length approximately 4, with 56 annuli. Hooks double, not dissected and measured.

(v) Three nymphs slide-mounted. Length about 5, with 56–58 annuli ($\bar{x}$ = 57). Hooks double, overall length 170–180.

(vi) Length about 5, with 56–61 annuli ($\bar{x}$ = 58). Hooks double, overall length 195–215.

Discussion

Riley *et al.* (1985) ascribed a double-hooked male nymph from the northern quoll, *Satanellus hallucatus* (Gould), to the genus *Waddycephalus* exclusively on the number of annuli, which vary from 55–78 in adult males of the genus (Riley & Self 1981b). This is considerably more than occurs in the two other genera which may have double-hooked larvae, *Elenia* and *Parasambonia* (Heymons 1939, Riley & Self 1982, Riley *et al.* 1985). All of the present specimens are placed in the genus *Waddycephalus* for the same reason, although specific identification is not possible.

The specimens from *D. rosamondae* probably belong to the same species, those from Abydos Station being at a slightly earlier stage of development.

The nymph from *R. remota* may be *W. punctulatus*. This species was first described from the common tree snake *Dendrelaphis punctulata* (Gray) in Australia (Riley & Self 1981b) but this host also occurs in New Guinea (Cogger 1983). The prey of tree snakes consist of frogs and birds, although reptiles and small mammals are occasionally eaten (Cogger 1983). Clearly frogs are probable intermediate hosts of *W. punctulatus*.

Either **Waddycephalus** or **Elenia** sp.

Material Examined

One nymph, from submandibular lymphatic sac of a frog, *Palmatorappia solomonis* (Sternfeld) Solomon Islands, in SAM No. N1985158.

Description

Male. Length 5, with 48 annuli. Hooks double, overall length 220–230.

Discussion

The generic status of this nymph is uncertain. *Waddycephalus komodoensis* and *W. radiata* are known from Indonesia (Riley & Self 1981b) and *Elenia vitiensis* is known from the Islands of Fiji (Heymons 1932). The low annulus count of the specimen may just preclude it being a species of *Waddycephalus*; the lowest annulus number known in mature males is 52, occurring in *W. komodoensis* (Riley & Self 1981b).

Armillifer sp. from snakes and rodents

Armillifer australis Riley & Self

Material Examined

(i) From viscera (the specimens probably inhabited the membranous lung which is often mistaken for the abdominal cavity) of a python (species unknown), South Australia, in SAM No. N1980207.

(ii) From lung of *Morelia amethistina* (Schneider), Melbourne Zoo, in SAM No. N1980206.

(iii) From lung of *Morelia spilota* (Lacépède), Queensland, in SAM No. N1980208.

(iv) From lung of *Morelia spilota* (Lacépède), Melbourne Zoo, in SAM No. N1980172.

(v) Encysted nymph from body cavity of *Rattus leucopus cooktownensis* Tate, Queensland, in SAM No. N1980209.

Description

(i) *Female* (n = 2). Length 63 and 67, both with 31 annuli and 2 incomplete annuli on terminal segment. Hooks removed from one side of one female, AC 410; AD 625 (Fig. 1D). *Male* (n = 2). Length 21 and 22, with 40 annuli; first 12 annuli with pair of projections pointing backward from posterior lateral angles.

(ii) *Female* (n = 15). Length 34–53 (one punctured female not included) ($\bar{x}$ = 42.5), with 29–32 annuli ($\bar{x}$ = 30.6) and 2 (or in two cases, 3) incomplete annuli on terminal segment. Hooks from a 49 mm specimen, AC 440; AD 635.

(iii) *Female* — mature (n = 1). Length 47, with 32 annuli (plus two incomplete segments terminally). *Female* — immature (n = 4). Length 16–27 ($\bar{x}$ = 19), with 29–32 annuli (plus 2 incomplete). *Male* (n = 3). Length 16–17, with 36–37 annuli, anterior 11–12 bearing backward-pointing projections.

(iv) *Female* (n = 1). Length 46, with 32 annuli (plus 3 incomplete).

(v) *Female*(?) (n = 1). Length 6, with 31 or 32 annuli. Hooks simple but could not be measured.

Discussion

Adult specimens from the four snakes are unmistakably *A. australis* and all characters accord perfectly with those of the type series (Riley & Self 1981a). *Morelia spilota* is a new host record.

Hooks of the nymph from *R. leucopus* are simple (i.e. without an accessory spine) and the annulus count is within the range (29–35) of mature female *A. australis* (Riley & Self 1981a). The present specimen almost certainly belongs to this taxon, as other species of *Armillifer* described from Australian hosts have more annuli (Riley & Self 1981a, Riley *et al.* 1985).

Discussion

In our earlier review of pentastomid parasites in Australian reptiles and mammals (Riley *et al.* 1985) we noted that the state of our knowledge of taxonomy is embryonic, and this is particularly true of the genus *Waddycephalus*. Our original finding of a double-hooked larva, which we attributed to the genus *Waddycephalus* rather than *Elenia* solely on the basis of the number of abdominal annuli, was the first implication of mammals as intermediate hosts in this genus.

This single male larva, from the mesentery of *Satanellus hallucatus* was cleared and mounted (Fig. 1B) and we observed that the sharp spinous extension overlying the hook appeared to be an integral part of it and separate from the fulcrum. This is unlike the situation in the related genus *Sambonia* where the accessory spine is clearly an extension of the fulcrum (Fain & Mortelmans 1960). The relative abundance of nymphal *Waddycephalus* material in the present study has permitted more detailed observations of hook morphology and these have confirmed our earlier interpretation. The spine is a functional part of the hook. It possesses an apodeme, onto which muscles attach and extend from it down into the fulcrum (contrast Figs 1C and D). The relative positions of the hook, its spinous extension and the fulcrum are presented diagrammatically (Fig. 2).

The seven species of *Waddycephalus* currently recognised in Australia infect boid, colubrid and elapid snakes (Riley & Self 1981b) which prey upon a variety of vertebrates (mostly frogs, lizards or mammals — see Cogger 1983) and the present report of *Waddycephalus* nymphs from these three classes of vertebrates is to be expected, particularly since vertebrate intermediate hosts are usual in porocephalid life-cycles (Nicoli & Nicoli 1966). Also, there is growing evidence from experimental infections (Esslinger 1962, Vargas 1970, Winch & Riley 1986), and from recoveries of nymphs in intermediate hosts (Sachs, Rack & Woodford 1973), that the definitive number of annuli is present in porocephalids by the infective stage. Our tentative diagnoses are based on the assumption that this occurs in the genus *Waddycephalus*. From the viewpoint of host dietary regimen, it is equally likely that the related genera *Parasambonia* and *Elenia* also utilize vertebrate intermediate hosts but in all cases, experimental evidence of these life-cycles is required.

Acknowledgments

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